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EARLY STAGES IN THE DEVELOPMENT OF CERTAIN PACHYPSYLLA GALLS ON CELTIS

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One of the most interesting angles from which the insect gall problem may be attacked is that involving the early stages of gall formation. The present study is a morphological one dealing with the beginning stages of two *Pachypsylla* (Fam. Psyllidae of the Hemiptera) galls as they develop on the leaves of the hackberry (*Celtis*).

THE GALLS

The galls concerned are common ones in their respective regions.

Pachypsylla mamma Riley is found on *Celtis occidentalis* L. It is a hemispheric to subcylindric outgrowth projecting from the under side of the hackberry leaf (Pl. XVIII, fig. 2). Above, on the opposite side, is a prominent depression, in the center of which is a minute conical process. Interiorly there is an inverted dome-shaped larval cavity lined by soft nutritive tissue; this latter in turn is invested by masses of hard, "protective" sclerenchyma. For a detailed discussion of the adult gall, the reader is referred to an earlier paper of the author's (8).

Pachypsylla asteriscus Riley occurs on *Celtis mississippiensis* Bosc. (fig. I, c, and fig. 7). It projects from both sides of the leaf, the part on the under side assuming the shape of a much abbreviated *Convolvulus* corolla, the part above consisting of a slender, straight process. These processes are attached to a blister-like enlargement in the plane of the leaf, in the interior of which is the lens-shaped larval chamber. Well defined layers of sclerenchyma occur in this gall, bounding the nutritive tissue.

Both of these galls are prosoplasmas or "higher" galls characterized by definite constitution and growth period and possessing highly specific forms and differentiation structures, which latter unusual characters are induced to appear under the action of the specific stimulus developed by the insect larva.

EARLIER WORK

No ontogenetical studies of the beginning stages of the galls formed by this genus of insects have heretofore been made. A few studies, however, have been made on the galls of other genera of the Hemiptera which may properly be presented here.

Prillieux (6) finds, in his study of the woolly apple aphid (*Schizoneura lanigera* Hausm.) gall on the apple twig, the following facts: No change

takes place in the cortical cells pierced by the proboscis of the insect other than the reaction to the mouth parts in them by laying down an "organic sheath" around these mouth parts. The living cells of the wood beneath the mouth parts proliferate strongly, building up a mass of hyperplastic parenchyma in which remnants of ducts are scattered. Multinucleate cells are reported present, but the author does not state in what cells this condition occurs.

Petri (4), in a comprehensive study of the grape *Phylloxera* root gall, finds the following phenomena to be exhibited: A "wartlike deposit" of calcium pectate is formed around the setae of the insect after their insertion, by the cytoplasm of the cells in which the setae are present. On the exterior of this sheath Petri believed he demonstrated a layer of tannic substance which upon oxidation gave the characteristic brown color to the old sheaths. The first important changes in the surrounding tissues are the sudden cessation of growth and the non-appearance of differentiation in all near-by cells. These cells show hypertrophy of their nuclei. A short distance from the mouth parts a "ringwall" of hyperplastic tissue springs up.

Rosen (7) studied the grape *Phylloxera* leaf gall with the following results: The initial depression is produced through "a lessened growth of the attacked mesophyll." "After three to four days of insect attack, the lower half of the leaf tissue which surrounds the portion in which the proboscis is inserted has proliferated enormously. The whole thickness of the leaf in the region immediately around the proboscis shows no proliferation. That portion of the leaf which is beneath the insect does not proliferate but the upper half at the sides of the insect grows upwards and forms the walls of a large insect cavity. Upper epidermal cells and several layers of mesophyll cells in the portion of the gall below the insect, show peculiar thickening and dissolution of their walls." "The investigation establishes the fact that the proboscis may pass through the entire thickness of the leaf." "The continuous sucking action by the insect at one fixed point for fifteen days is believed to be the initial stimulus for gall development."

METHODS

The material of *Pachypsylla mamma* and observational data concerning it were obtained in and near Manhattan, Kansas. That of *P. asteriscus* was acquired in northeastern Texas.

At the critical time in the spring, hatching of the nymphs and gall initiation were observed in the field and laboratory, making possible the fixation of gall material in its earliest stages. All material was fixed in weak chromoacetic killing fluid (Schaffner's formula), embedded in paraffin, cut 10 microns thick and stained with Flemming's triple stain. All histological drawings were made with the aid of a camera lucida.

INITIAL STAGES OF THE GALLS

Before attacking the problem of primary cecidium ontogenesis, a very brief statement of the life history of the insect will be given leading up to gall initiation. The following deals with *P. mamma*. *P. asteriscus* has an almost identical life history.

The adults, which are formed immediately after the escape from the galls of the fully grown nymphs in the fall of the year, overwinter in the bark crevices or in ground debris. After mating in early spring, the females lay their eggs on the under side of the young leaves as they begin to protrude from the buds. The point at which the egg is attached is commonly killed, this killing resulting in a prominent hole in the mature leaf. This explains, in part, the presence of numerous perforations in gall-infested leaves. The minute oval eggs (0.3 mm. long) hatch in 2-3 days, the nymph immediately migrating to the upper side of the very young leaf, where, after reaching a position near a principal vein, it settles down to initiate gall development. Once the growing gall has engulfed it, it is a prisoner until its escape the following fall as a mature nymph.

The nymph at the time of gall initiation is a minute, salmon-colored, flattened insect, oval in outline, and measures 0.22 mm. in length. On the ventral side, the setae, which in this minute insect are perfectly formed, extend from the body at a place slightly anterior to the median point. The setal puncturing mechanism measures but little over 1 micron in transverse diameter. There are no special structural modifications in these gall-making nymphs which distinguish them from the large numbers of non-gall-forming Hemipterous larvae.

Under the binocular microscope, the early superficial conditions in gall development may be easily observed and are as follows: The insect's body is pressed close to the upper side of the leaf; a shallow downward evagination forms, lowering the insect into the body of the leaf; when the upper side of the insect has been lowered to the level of the leaf surface, a very rapid upward growth of the leaf tissue surrounding the insect takes place, appearing first like a crater but finally as a closed cone completely covering the nymph. Both *P. mamma* and *P. asteriscus* galls are characterized in their initial stages by this combination of the diverticulum and walled conditions ("Umwellungen" of Küster). The *P. mamma* gall in its further development emphasizes the diverticulum character, the original "cover-cone" developing but slightly, while in the case of *P. asteriscus* no prominent evagination occurs but the cover-cone grows into the prominent, slender, subcylindric process so characteristic of this gall.

HISTOLOGICAL PHENOMENA

At the time when the nymph inserts its setae into the embryo leaf, the leaf cells are not in the primordial condition of undifferentiation but show

distinct though partial differentiation; the upper epidermis is very well defined, being composed of large cuboidal cells (fig. 3, at right); the mesophyll shows three distinct layers, and the lower epidermis is set off from the other layers by the minute size of the units composing it. The chloroplasts of the mesophyll cells are well developed as to size and number.

A number of modifications occur coincidentally following the insertion of the setal proboscis. These are: (1) The reaction of the cytoplasm of the cells penetrated by the setal structure to this foreign structure, by laying down around it a deposit of organic substance in the form of a very thin, uniform membrane. This structure thus constitutes a definite sheath. (2) A marked hypertrophy of the lower epidermal cells and in a lesser degree of the adjacent mesophyll cells. (3) Hyperplasia sets in in the middle region of the mesophyll surrounding the end of the proboscis. This, however, is greatly restricted. In the case of the *P. mamma* gall (fig. 3), wall formation accompanies the nuclear divisions almost invariably in the early stages; while in the case of *P. asteriscus* wall construction does not occur, the original cells of the mesophyll tiers thus being left almost undisturbed, the cells, however, containing many nuclei. This is best demonstrated in a somewhat later stage (fig. 5b). (4) Partial degeneration of the chloroplasts of cells beneath the insect, involving loss of chlorophyll and more or less reduction in size. (5) An increase in the size of the nuclei as compared with those of the normal parts.

The total result of the early hypertrophic and hyperplastic changes is the formation of a saucer-shaped depression in which the nymph (not shown in section) passively lies (fig. 3). This depression or evagination is produced chiefly through the hypertrophy of the elements on the under side of the leaf or that opposite to the insect.

Figure 4 presents a median section of a later stage of the *P. mamma* gall. It will be noted that, compared to the tissue lying at some distance from the larva, the tissue immediately beneath the insect and adjacent to the proboscis shows a marked inhibition of cell-divisional activity. This condition is very characteristic of both galls. These non-dividing cells, however, show the same high protoplasmic content that the actively dividing cells do, so that, when the section is viewed as a whole, there appears to be a zone of meristematic tissue traversing the young gall (shaded cells, fig. 4).

The whole situation, despite the fact of the local growth inhibition mentioned, when contrasted with the condition in a normal partially differentiated leaf, shows that in the early stages of cecidogenesis a process of dedifferentiation is going on, throwing the tissue back into a homogeneous condition. Were events to stop here (fig. 4), we should have a typical kataplasma showing the retrogressive changes of that type of overgrowth. The gall in its further development, however, differentiates into a highly specific prosoplasma, thus furnishing a characteristic example of gall ontogeny recapitulating gall phylogeny.

A still older stage (1 mm. long diameter) of a *P. mamma* gall (median section) is shown in figure 9. The cover-cone has attained almost its maximum size (in the adult gall it is a minute papilla), and the characteristic sub-hemispheric form of the gall has definitely appeared. The occurrence on the very young galls of the large trichomes is worthy of note. These are highly evanescent, never being seen on the adult structure. A presentation of the histology of the nearly mature gall is given in an earlier paper of the writer's (8).

The early histogenesis of a *P. asteriscus* gall is different from that of the *P. mamma* gall. The differences are of course related to the specificity of the galls.

Figure 5 shows the outline of a median section of a very young *P. asteriscus* gall (1 mm. long diameter). At this early stage the fundamental form of the mature gall (fig. 7) is appearing in the prominent cover-cone, the circular outgrowth beneath which in section is exhibited as two lateral processes. The thickness of the region beneath the insect is definitely less than that of the normal leaf as seen to left and right, indicating a marked inhibition of growth in those tissues.

In figure 5a are presented the tissue conditions of a critical portion of the section shown in figure 5. Here, as in the case of the *P. mamma* gall, a meristem-like layer is well defined. The details of these two layers and other cellular features are shown in figure 5b, which presents the region immediately surrounding the mouth parts. This region, it will be noted, with the exception of a small portion of it directly beneath the sheath-enclosed mouth parts, has maintained the original five-layered condition of the young leaf. Though slightly excessive nuclear division has taken place in the zone of growth inhibition, wall formation has not occurred, the result being the appearance of multinucleate or "giant" cells, the largest of which is that one in which the end of the proboscis terminates. The presence of such a giant cell as the one last mentioned, is also noted in the *P. mamma* galls (fig. 6). Further discussion of this giant cell situation will be given later.

Rosen (7) found an inhibition of growth in the floor of the grape Phylloxera leaf gall but reports no multinucleate condition.

Differing in still another character from the *P. mamma* gall, that produced by *P. asteriscus* shows the very early differentiation of a sclerenchyma layer through the deposition on the walls of the lower hypodermal cells of bands of lignin, simulating the scalariform type of lignification (fig. 5b).

The curious condition of the cell in the upper right-hand corner of the section (fig. 5b), the cell being almost empty and a rivet-shaped plug of deeply staining matter inserted in the wall, is undoubtedly due to mechanical puncture by one of the two stout bristles with which each leg of the nymph is armed. More injury of this character does not occur probably because of the extreme passivity which characterizes the insect throughout the period of gall formation.

THE SHEATH

The results of this study are in accordance with Prillieux's (6) and Petri's (4) observations that an organic membrane is deposited by the cytoplasm around the setal proboscis (figs. 5*b*, 6, 8, 10). I found as did Petri in the grape *Phylloxera* root gall that this membrane is composed of calcium pectate, but was unable as he was to demonstrate a layer of tannic substance on its exterior. In Petri's material the deposit was irregularly laid down or, as he described it, appeared "warty," while in mine it was deposited with remarkable uniformity as to thickness. This sheath is open at its end, thus making possible the direct movement of cellular substances into the end of the setal proboscis. This opening can be demonstrated only with the oil immersion objective in favorable sections (fig. 5*b*), for in many instances the end of the tubular sheath is surrounded by a dense mass of cytoplasmic granules. The nature of this mass I was unable to determine.

Figure 8 illustrates a case in which the insect partially withdrew the setae, then plunged them in again in a different direction. Figure 10 shows an extremely rare condition in which the nymph has withdrawn the mouth parts completely and twice reinserted them. The setae were found as shown, broken off and sticking in the shortest of the three sheaths. The middle sheath is distinctly abnormal. This section shows a condition commonly observed, *viz.*, the projection of the sheath structure beyond the surface of the outer cells.

Examination of half-grown galls and of older ones has shown but one sheath present, indicating that but one insertion of the proboscis takes place, the insect remaining passive and maintaining a stable position for relatively long periods of time. Rosen (7) found the same to be true in the grape *Phylloxera* leaf gall. Rosen's figure 4 shows a perfect sheath which he inadvertently misinterpreted as "proboscis."

Since in all studies to date of Hemipterous insect cecidiogenesis, an organic sheath has been found surrounding the setal mouth parts, we have reason to believe that the phenomenon is a general one for that group of zoocecidia.

MULTINUCLEATE CELLS

Multinucleate or giant cells are not unknown in gall tissues, and even are not absent from normal tissues according to Beer and Arber (1), who have found the phenomenon in the stems of 50 dicots and 17 monocots. Prankerd's (5) studies of the occurrence of multinucleate cells in normal tissue are of interest in this connection. He believes they are mostly formed by amitosis. He finds in many instances that a wall is formed later by the two protoplasts resulting from a single amitotic division. Küster (3) presents a number of records of cecidial giant cells in many of which amitosis is reported as the mode of origin of the nuclei. In one instance, the *Erineum*

mite gall on the leaf of the European linden, Küster found, in addition, the degeneration of one nucleus to be a constant phenomenon.

The multinucleate cells found in this study are of much interest, not only because such cells have been rarely reported in the higher galls, but also because a special situation was found in which many of the nuclei were undergoing a process of disintegration.

In the *P. asteriscus* gall, by the time the gall has attained a length of 1 mm., many of the cells, both the one in which the stylets end and certain of those in the immediate neighborhood, show more than one nucleus (fig. 5*b*). The median cell holding the opening of the sheath-enclosed proboscis has generally the largest number, as many as four to six being visible in one focal plane. The other cells possess fewer, more than two being seldom found definitely showing in the same focal plane. Only a few cells in such a section as shown in figure 5*b* are thus seen (oil immersion lens), but these are unmistakably multinucleate.

The nuclei within a particular cell upon critical examination do not appear to be all in the same condition. One commonly, or at the most two of them, may be regarded as normal, while the others exhibit varying stages of disintegration (fig. 5*c*, scale same as fig. 9*a*). In this disintegration process the nuclear membrane disappears, and a prominent vacuole develops in place of a part or all of the nuclear body. The nucleolus persists quite unchanged and may often be found stranded in the cytoplasm near a vacuole.

In the 1 mm. gall of *P. mamma* practically no multinucleate cells are found aside from the large central one in which the mouth parts terminate. But in much older material (the half-grown gall) excellent examples of the giant-cell condition are found. In these, as in the cells of the *P. asteriscus* gall, all stages of disintegration of the nuclei excepting one or two are plainly evident (fig. 9*a*). The problem of the mode of origin of these nuclei is an important one since in some instances, such as the giant cells of the nematode (Heterodera) galls, nuclear proliferation has been reported as amitotic in character. After a most painstaking examination of my slides I am strongly inclined to interpret the situation in terms of amitosis. I am not able, however, to furnish direct positive proof.

The total absence of mitotic figures from the cells of the region concerned might be due merely to the fact that this region is characterized by a marked inhibition of growth as compared to adjacent regions. Individual cells having their origin in the normal embryo leaf before the insect's attack, later, under the inhibiting influence exercised on the three cell layers beneath the nymph, retain their integrity even into the adult gall stage, changing only in the matter of numerical nuclear increase.

This latter change is then followed by degeneration of certain of the nuclei. Since the number of nuclei per cell is always relatively low, seldom if ever going over eight, and since the divisions producing these are scattered

over a relatively long period of time (one to four weeks roughly), the chances of catching a nucleus in the act of division are very remote. This of course is true whether the division is of the mitotic or of the amitotic type. For this reason if for no other it is impossible to determine definitely the nature of the nuclear cleavage.

The evidence for amitosis is of an indirect character, such as the frequent occurrence of lobulate nuclei; the very rare display of a constricted nucleus; the frequent occurrence of two nuclei in contiguity; and the very irregular distribution of the nuclei in the cell. But, as heretofore stated, the extremely high infrequency of divisions of any kind makes it quite impossible to determine the nature of the divisions definitely.

DIFFERENTIAL GROWTH BETWEEN LARVA AND GALL

Data should be given concerning the difference in time of occurrence of the grand periods of growth of the larva and gall respectively, as this is a matter of more than passing interest. This difference is readily brought out by the following table:

Measurements of larva and gall at different stages of their concomitant development

	Width of larva	Height of gall
Stage 1.....	0.20 mm.	0.14 mm.
Stage 2.....	0.22 mm.	0.80 mm.
Stage 3.....	0.31 mm.	3.55 mm.
Stage 4.....	0.40 mm.	3.75 mm.
Stage 5.....	1.69 mm.	5.00 mm.

The grand period of growth for the gall is that of its early existence, while that of the larva comes later when the gall is more than half grown. This inhibition of growth in the larva for an extended period, which is coincident with gall morphogenesis, is in the mind of the writer a very significant phenomenon. Just what it implies in its entirety is quite unknown, but we may feel reasonably sure that it is related in some manner to the production of the gall-making stimulus. The energy of the larva appears at first to be consumed in producing the stimulus, and only when gall development is well on its way to maturity is this energy released for the anabolic processes of the larva itself. This is of course but an assumed generalization which cannot be proved until the problem of the nature of the stimulus involved has been cleared up.

THE STIMULUS PROBLEM

In many instances the discovery of special structures has been of much value in interpreting function. When we raise the physiological problems of the nature of the gall-forming stimulus in these prosoplasmas and look for some hints concerning it from structural conditions, it must be confessed that none are given. I cannot find a single structural fact produced by

any one in the study of the initial stages of Hemiptera galls, that throws any light whatever upon the profound problem of the nature of the highly specific stimulus applied by the insect to the embryonic plant tissue.

Rosen's (7) "belief" that "the continuous sucking action by the insect at one fixed point for fifteen days is the initial stimulus for gall development" will not hold, for there are too many non-gall-making hemipterous insects sucking at one place for extended periods without ensuing hypertrophy or hyperplasia. Further, as previously shown, little or no ingestion takes place, for in the early days of its gall-making activity no increase in size of the larva occurs. It is hardly conceivable that the pumping action of the insect's sucking apparatus would function without ingestion going on, especially when the proboscis end was in the presence of liquid or semi-liquid food. Attention may also be called to the fact that no experimental evidence along this line has yet been produced.

On a *priori* grounds it would seem much more natural to assume with Küster that such prosoplasmas were "*Chemomorphosen*"; that a highly specific chemical substance was introduced producing the radial effects noted. This conception, however, has not the slightest direct evidence for its support, since such a specific chemical substance producing a prosoplasma has never been demonstrated. The difficulty of demonstrating it may be of course due only to the exceedingly minute amounts of it which are formed. Conservatism here as elsewhere is the desirable position to assume.

One who has repeatedly removed these minute, delicate gall-inciting organisms from the plastic, watery tissue of the embryonic galls is impressed with the possibility of interpreting the situation in terms of correlation phenomena. The writer ventures to suggest that the insect may be acting as a whole in the matter.

Though the structural facts concerning gall initiation and early development are of much interest, we must confess that these data give us no more fundamental, explanatory information concerning gall ontogenesis than do the structural facts of normal growth explain normal ontogenesis. We must remain satisfied with having merely demonstrated the leading morphological facts involved in the early development of these two Pachypsylla galls.

SUMMARY

1. The early stages of two hemipterous insect galls of the hackberry leaf were studied. The insects belong to the genus Pachypsylla of the Psyllidae.

2. The newly hatched nymphs after placing themselves upon the upper side of the young leaf initiate the following concomitant changes: (a) Formation by the cytoplasm of the affected cells of a sheath-like structure around the inserted setal proboscis. The cells are not killed. The pro-

boscis is inserted but once, the larva retaining its position through the period of gall development. (b) Hypertrophy of the epidermal and adjacent mesophyll cells on the lower side of the leaf opposite to that attacked by the insect. (c) A slight hyperplasia generally appears in the cells immediately surrounding the end of the mouth parts. (d) Degeneration of chloroplasts in a zone beneath the larva. (e) An increase in the size of the nuclei in the same zone.

3. The above noted changes (b and c) produce a downward evagination which lowers the insect into the body of the leaf, after which process a "cover-cone" rapidly grows over it, springing from the tissue surrounding the larva.

4. Multinucleate cells appear in the tissue of the floor of the larval chamber, most of the nuclei, however, soon disintegrating. The mode of origin of these nuclei is believed to be amitotic, though this under the condition of high divisional infrequency cannot be definitely proved.

5. The very early differentiation of a sclerenchyma layer, one cell in thickness, is highly characteristic of one of the galls.

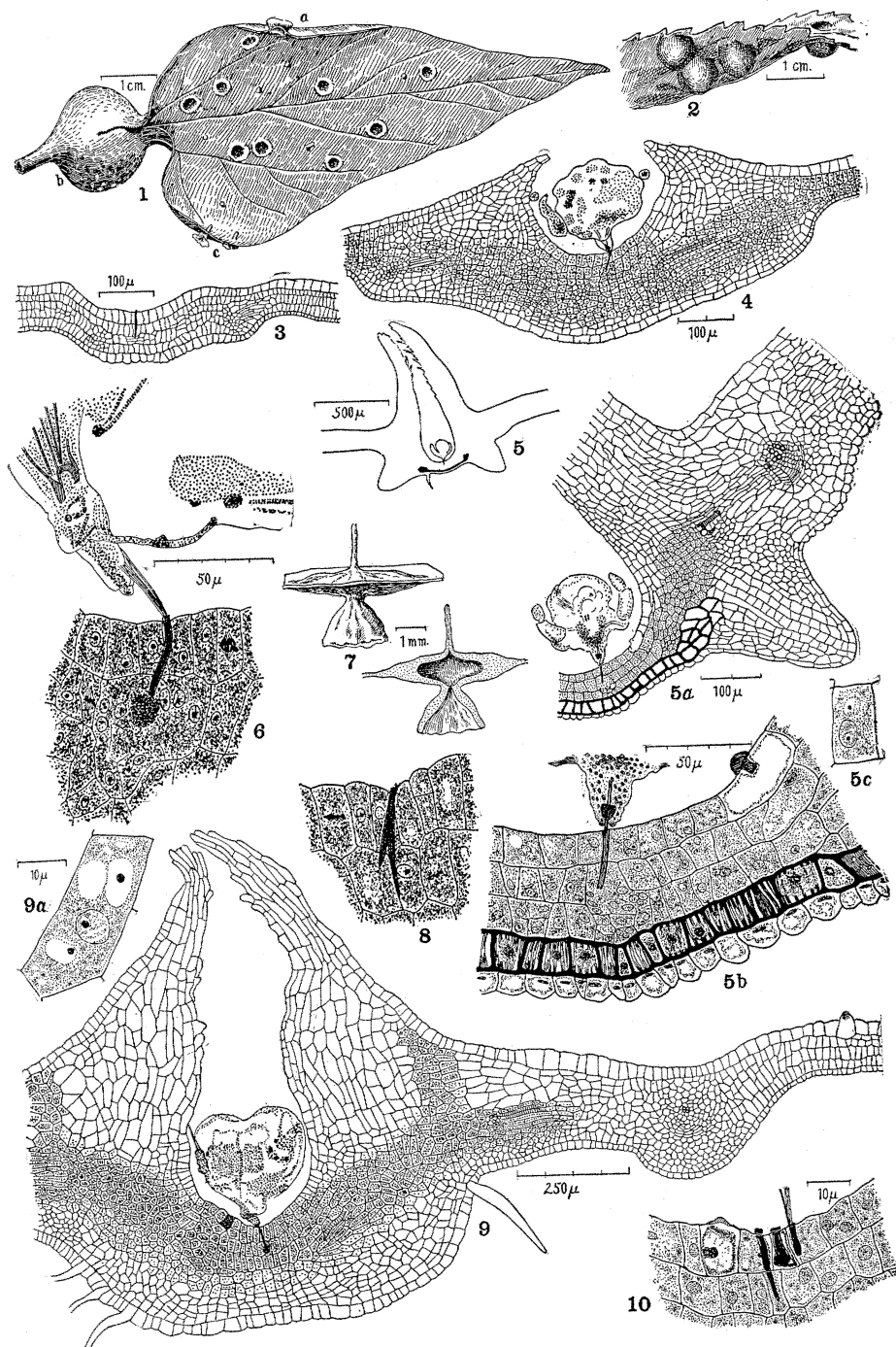
6. The nymph shows practically no increase in size until the gall is about half developed. Thus the grand period of growth in the gall is at the beginning of its ontogeny while that of the insect is postponed until cecidogenesis is well under way.

7. The morphological facts discovered furnish no assistance whatever in the formulation of a theory concerning the nature of the stimulus used by the larval insects in initiating and carrying to completion the highly specific gall structures characteristic of the two species respectively.

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WELLS: EARLY STAGES IN THE DEVELOPMENT OF PACHYPSSYLLA GALLS.

EXPLANATION OF PLATE XVIII

FIG. 1. Leaf of *Celtis mississippiensis* showing three distinct types of Pachypsylla galls: (a) Variety of *P. mamma*. (b) Compound gall of *P. venusta*. (c) Gall of *P. asteriscus*.

FIG. 2. Galls of *P. mamma* (typical form) on *Celtis occidentalis* leaf.

FIG. 3. Earliest initial stage of the *P. mamma* gall.

FIG. 4. Early stage of *P. mamma* gall.

FIG. 5. Outline of longitudinal section of early stage of gall of *P. asteriscus* (1 mm.).

FIG. 5a. Tissue study of lower right-hand portion of section shown in figure 5.

FIG. 5b. Cell study of region around mouth parts shown in figure 5a.

FIG. 5c. Multinucleate cell from same gall as figure 5 showing two nuclei, one of which has partially disintegrated.

FIG. 6. Detail from section of very young *P. mamma* gall; setae partially withdrawn from sheath.

FIG. 7. Gall of *P. asteriscus*, external and internal views.

FIG. 8. Detail from section of very young *P. mamma* gall showing the forked sheath formed through withdrawal and reinsertion of the setae.

FIG. 9. Section of very young *P. mamma* gall (1 mm.).

FIG. 9a. Cell from half grown *P. mamma* gall showing multinucleate condition. Note nuclei which show a degenerate condition.

FIG. 10. Detail from section of very young *P. asteriscus* gall showing three sheaths (more than one is extremely rare); setae still inserted in one to right.